

蝶と蛾 *Tyô to Ga*, **41** (3) : 193–199, 1990

The Unknown Male of *Tiradelphe schneideri* (Lepidoptera, Danainae) — Missing Piece in a Butterfly Puzzle

R. I. VANE-WRIGHT

The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

and

Michael BOPPRÉ

Forstzoologisches Institut der Universität Freiburg, Fehrenbühl 27,
D-7801 Stegen-Wittental, Fed. Rep. of Germany

Abstract *Tiradelphe schneideri*, first described in 1984 as a new genus and species within the Danaini, is still only known from two female specimens from Mount Popomanaseu, Guadalcanal, in the Solomon Islands. Cladistic analysis has placed *Tiradelphe* in an unresolved group with *Danaus* and *Tirumala*. Discovery of the unknown male of *Tiradelphe* is therefore expected to shed new light on the evolution of these butterflies, including their chemical communication.

Key words *Danaus*, *Tirumala*, *Tiradelphe*, evolution, chemical communication, pheromone-transfer-particles, androconial systems, Guadalcanal.

Introduction

Tiradelphe schneideri ACKERY & VANE-WRIGHT, 1984 (Fig. 1), first described as a new genus and species of milkweed butterfly (Danainae), is still only known from two female specimens from Mount Popomanaseu, Guadalcanal, Solomon Islands. In their original cladistic analysis, ACKERY & VANE-WRIGHT (1984) placed *Tiradelphe* in a monophyletic group with *Danaus* and *Tirumala*. Recently, BOPPRÉ & VANE-WRIGHT (1989) have drawn attention to remarkable differences in the androconial systems of *Tirumala* and *Danaus*. These differences are so abrupt that it is difficult to imagine a gradualistic model to account for the evolutionary changes that appear to have taken place. Discovery of the male of *Tiradelphe*, the rarest of all known danaines, is highly desirable, in that knowledge of its androconial system will provide new insights into the evolution of these butterflies, including their chemical communication.

Chemical communication in milkweed butterflies

Chemical communication by male milkweed butterflies exhibits a number of remarkable features, including the use of pheromone components synthesized from secondary plant compounds (pyrrolizidine alkaloids) actively gathered by the male adults (review: BOPPRÉ, 1986), and complex dual or binate androconial systems

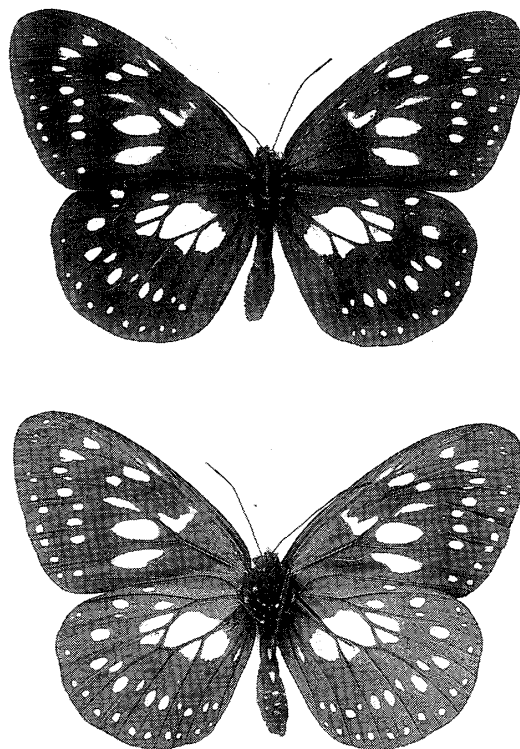


Fig. 1. Holotype female of *Tiradelphe schneideri* ACKERY & VANE-WRIGHT, 1984.
Forewing length: 46 mm. Above: upperside; below: underside.

involving eversible abdominal hairpencils and wing organs. In the Danaini, a tribe comprising one half of the subfamily, most of the 83 species have androconia that produce cuticular pheromone-transfer-particles ("love dust"), scattered from the hairpencils and stuck to the female antennae during courtship. The exact significance of this elaborate system is not yet understood (BOPPRÉ, 1984; BOPPRÉ & VANE-WRIGHT, 1989).

The evolution of PTP production in the Danaini

Amongst the six currently recognized genera of the Danaini, only one is known not to include species which produce pheromone-transfer-particles (PTPs) : based on knowledge of both morphology and behaviour, none of the eight species of *Ideopsis* does so. The situation in *Tiradelphe* is unknown, as the male has yet to be discovered.

Given the wide distribution of PTP production within the Danaini, and its absence in the remainder of the subfamily and the closely related Ithomiinae and Tellervinae, ACKERY & VANE-WRIGHT (1984 : 39) suggested that the ability to produce PTPs was a basic ("ground-plan") feature of the tribe. If so, PTPs would be homologous throughout the group. However, BOPPRÉ & VANE-WRIGHT (1989) have described three quite distinct modes of PTP production within *Amauris ochlea* BOISDUVAL, 1847,

Danaus chrysippus LINNAEUS, 1758, and *Tirumala petiverana* DOUBLEDAY, 1847.

In *Amauris ochlea* PTPs are produced by splitting of the terminal parts of the "long white hairs", one of five hair-types found in the abdominal hairpencils of this species. In *Danaus chrysippus* PTPs are produced by distinct "particle budding hairs" which, unlike the long white hairs of *Amauris*, do not break up but, instead, give rise to similarly large numbers of PTPs by shedding buds. In *Tirumala petiverana* no particles at all are produced within the abdominal hairpencils; instead, large quantities of polyhedral PTPs are generated within the alar organs (hindwing cubital pouches in *Tirumala*) by the fragmentation of extremely long "cushion scales" (homologous structures occur in the wing organs of *Amauris* and *Danaus*, but they are much smaller and stable, not disintegrating into particles).

These observations (BOPPRÉ & VANE-WRIGHT, 1989), together with the fact that no intermediate types of particle producing systems have been observed, strongly suggest (*contra* ACKERY & VANE-WRIGHT, 1984) repeated parallel evolution within these closely related genera, not that PTPs have evolved by successive modification of a ground-plan feature inherited directly from a common ancestor. Other outstanding differences occur between the androconial systems of *Danaus* and *Tirumala*.

In both of these genera the abdominal hairpencils interact with pocketed hindwing cubital organs, the separate glands being brought into contact by special behaviour temporally independent of courtship. While in *Tirumala* this serves to transfer the PTPs from their site of origin in the cubital pouches to the hairpencils, from where they are eventually deployed as love dust during courtship, in *Danaus* (producing PTPs within the hairpencils) contact-behaviour serves the biosynthesis of physiologically normal amounts of the pyrrolizidine-alkaloid-derived pheromone component (BOPPRÉ *et al.*, 1978); the binate interaction in *Tirumala* may also serve a chemical function in addition to PTP transfer, but this has not been demonstrated.

Furthermore, although *Tirumala* and *Danaus* uniquely share pocketed cubital hindwing androconial organs, the in-pocketing during wing expansion after eclosion proceeds quite differently in the two genera, to form a "pocket" in *Danaus* and a "pouch" in *Tirumala* (BOPPRÉ & VANE-WRIGHT, 1989). This suggests that the pocketed condition may also have evolved quite independently in the two genera.

We are thus left with an outstanding puzzle. If PTP production and alar organ in-pocketing have both evolved independently in *Danaus* and *Tirumala*, what explanations can be offered to account for these remarkable parallelisms? Alternatively, if we consider the possibility that the *Danaus* type of androconial system evolved from a condition comparable to modern *Tirumala*, or vice versa, how could it be that one system of PTP production was abandoned and substituted by another?

The great significance of the unknown male of *Tiradelphe schneideri* lies in the fact that, according to the cladistic analysis of ACKERY & VANE-WRIGHT (1984), this rare butterfly forms an unresolved monophyletic group with *Danaus* and *Tirumala*. Thus, if *Tiradelphe* had not been discovered, we would have no hesitation in regarding *Danaus* and *Tirumala* as sister genera (FORBES, 1939; ACKERY & VANE-WRIGHT, 1984; KITCHING, 1985). From a comparative point of view, and with no evidence from fossils,

this would have left us with little hope of making further sense of the outstanding differences in their androconial systems. However, depending on the eventual resolution of the phylogenetic (cladistic) relationships of *Tiradelphe*, *Danaus* and *Tirumala*, analysis of male *Tiradelphe* will shed considerable light on this problem.

Three configurations

Three resolutions of the cladistic relationship of *Tiradelphe* to *Danaus* and *Tirumala* are possible. Based on present knowledge (BOPPRÉ & VANE-WRIGHT, 1989), we consider the following three configurations for the unknown androconial system of *Tiradelphe* to be the most likely :

1) the same androconial system as *Danaus* (2 types of hairpencil hair, one producing PTPs; alar pocket); 2) the same androconial system as *Tirumala* (1 type of hairpencil hair; alar pouch producing PTPs from cushion scales); or 3) unique androconial system (1 type of hairpencil hair; no PTPs in either organ; open cubital glandular area).

If *Tiradelphe* is the sister of *Danaus*, then its possession of androconial system 1) would offer no new insight into the quantum shift between the *Danaus* and *Tirumala* systems; 2) would indicate that the *Danaus* system had evolved from a *Tirumala*-like condition; while 3) would indicate that they had evolved independently. Alternatively, if *Tiradelphe* is the sister of *Tirumala*, then possession of androconial system 1) would suggest that the *Tirumala* system had evolved from a *Danaus*-like system; 2) would be uninformative; while 3) would again indicate independent evolution. Finally, if *Tiradelphe* should prove to be the sister of (*Tirumala* + *Danaus*), then 1) would imply that the *Tirumala* system evolved directly from a *Danaus*-like stage; 2) that the *Danaus* system evolved from a *Tirumala*-like condition; while 3) would be uninformative with respect to *Danaus* and *Tirumala* – we would still be uncertain as to

Table 1. The implications for the evolution of the androconial systems of *Danaus* and of *Tirumala*, dependent on the three possible resolutions for the cladistic relationship of *Danaus*, *Tirumala* and *Tiradelphe*, and the three androconial configurations considered likely for *Tiradelphe* (see text). AS = androconial system.

	<i>Tiradelphe</i> with AS like <i>Danaus</i>	<i>Tiradelphe</i> with AS like <i>Tirumala</i>	<i>Tiradelphe</i> with AS unique
<i>Tiradelphe</i> sister to <i>Danaus</i>	—	<i>Danaus</i> AS evolved from <i>Tirumala</i> -like AS	<i>Danaus</i> and <i>Tirumala</i> AS evolved independently
<i>Tiradelphe</i> sister to <i>Tirumala</i>	<i>Tirumala</i> AS evolved from <i>Danaus</i> -like AS	—	
<i>Tiradelphe</i> sister to (<i>Danaus</i> + <i>Tirumala</i>)		<i>Danaus</i> AS evolved from <i>Tirumala</i> -like AS	—

whether or not the two systems evolved independently, or if one system had undergone some transformation, one into the other. These possibilities are summarized in Table 1.

The need for new data

Milkweed butterflies belong to the best investigated Lepidoptera, having been intensively studied from a variety of evolutionary, chemoecological and sociobiological viewpoints. Thus, the puzzle discussed here is embedded in a much more general context, and many more reasons could be given to stress the exceptional relevance the discovery of male *Tiradelphe schneideri* will have for our understanding of the biology of the milkweed butterflies, amongst which *Danaus* and *Tirumala* are outstandingly important genera.

Independent data concerning the cladistic relationships of *Tiradelphe* will be essential for a successful solution to the *Tirumala* and *Danaus* puzzle. This is because a number of the characters used in the original analysis (ACKERY & VANE-WRIGHT, 1984) stem from the very androconial systems that are here the focus of interest. Following the discovery of male *Tiradelphe*, it will be necessary to eliminate these characters from further cladistic analyses. New characters should be sought from any available sources, including early stages and chemistry (such as pheromone bouquet volatiles : cf. SCHULZ *et al.*, 1988).

The search to rediscover *Tiradelphe schneideri*

Tiradelphe schneideri was discovered on Mount Popomanaseu during 3–6 November 1965 [not “October”, as stated in ACKERY & VANE-WRIGHT, 1984] , by native porters working for a British Royal Society Solomon Islands expedition. They collected the two female specimens from open vegetation at about 2300 m, just below the mountain summit (visiting the actual summit is prohibited by local taboo). Other butterflies collected at the same time included another rare danaine, *Parantica garamantis* GODMAN & SALVIN, 1888, and a new species of *Delias* (since described by ARORA, 1983).

Females of *Tiradelphe schneideri* are recognizable by their rounded wing shape, and relatively large size (forewing length about 45 mm). According to ACKERY & VANE-WRIGHT (1984: 151), *T. schneideri* belongs to a small mimicry ring involving female *Euploea tulliolus pyres* GODMAN & SALVIN, 1888, *Ideopsis juvena sobrinoides* BUTLER, 1882, *Parantica garamantis* and *Tirumala hamata obscurata* BUTLER, 1874. Of these, *P. garamantis* is the only species likely to be encountered at the same altitude ; it has more angular wings, the hindwing discal cell is narrower, and the forewing has a distinct pre-apical pale fascia. The female of *E. tulliolus pyres* is perhaps the most similar to *Tiradelphe* in overall appearance ; the *Euploea* is smaller (forewing length less than 40 mm), and its hindwing discal cell extends well beyond the mid-point of the wing (female *Tiradelphe* has the hindwing discal cell only just reaching the wing mid-point).

Despite the fact that thousands of milkweed butterflies have been collected from Guadalcanal, *T. schneideri* was never discovered before 1965, nor has it been collected again since. Mount Popomanaseu and the other high peaks on the island (e. g. Mount Gallego) are not only protected in some cases by taboos, they are also physically very difficult to ascend, being subject to frequent landslips. The Royal Society Expedition, which was on Popomanaseu from 14 October – 15 November 1965 (CORNER, 1969: 626), remains one of the few successful biological excursions to this inaccessible region.

Many species of Danainae are lowland insects, only rarely occurring above 1000 m. However, there are some more specialized mid-montane species which fly from about 1000 – 3000 m, including a number of *Euploea*, *Anetia*, *Ideopsis* and *Parantica* normally found at 1500 – 2300 m (ACKERY & VANE-WRIGHT, 1984). Amongst these is *Parantica garamantis*, known only from the mountainous region of Guadalcanal, in the eastern Solomons, and Bougainville (Papua New Guinea) at the opposite, western end of the Solomons archipelago. *Delias messalina* ARORA, 1983, in addition to being found on Mount Popomanaseu, is also known from Bougainville (1250 m) and Santa Isabel. From this we predict that *Tiradelphe* is probably restricted to montane habitats and is unlikely to be found much below 1500 m. Very possibly it occurs only in the mountains of central Guadalcanal but, if it does prove to have a wider range, the most likely additional location will be at mid-montane to high elevation on Bougainville.

In the light of this, anybody intending to undertake the arduous and difficult journey required to rediscover *Tiradelphe schneideri* should plan to gather adequate samples. These would include not only conventional dried specimens for gross morphology but also, if sufficient material is at hand, specially prepared hairpencils for chemical investigations and (ideally) live material for possible DNA work. At the same time every effort should be made to discover the early stages and hostplant(s) of this, the rarest and potentially most interesting of all milkweed butterflies, and to investigate whether or not it is attracted to pyrrolizidine alkaloids.

We invite anybody who might plan to undertake such an expedition with the purpose of rediscovering *Tiradelphe schneideri* to contact us to discuss the requirements and techniques in more detail.

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摘 要

未知なる *Tiradelphe schneideri* のオス—蝶のジクソーパズルにおける失われた一片
(R. I. VANE-WRIGHT & Michael BOPPRÉ)

マダラチョウ亜科における科学的コミュニケーションとは、♂が特別に集めた植物の二次的化合物に由来するフェロモン成分，ならびに複雑な雄発香器官のシステム(androconial system) [ヘアーペンシルや性斑]を含む，いくつかの顕著な特殊化のことを意味する．マダラチョウ族においては，大部分の種の雄発香器官は，求愛時に「媚薬」として用いられる「フェロモン移送粒子」(PTPs)を生成する．この「フェロモン移送粒子」は，属が異なれば，とくに *Danaus* と *Tirumala* の間では，まったく異なった方法で生成され，この粒子が平行進化によって生じたことを強く示唆する．今のところ，これについて何らかの説明を与えることはできないが，もしできるとするならば，このような特殊化したシステムが進化的形質転換系列をつぎつぎ経てきたという可能性だけである．

Tiradelphe schneideri は1984年マダラチョウ族に含まれる1属1種の新種として記載され，いまだにソロモン群島ガダルカナル島のPopomanaseu山で得られた2♀の標本が知られているのみである．分岐学的分析によると，*Tiradelphe* は *Danaus* と *Tirumala* とともに1単系統群に暫定的に含められた．それゆえ，未知なる *Tiradelphe* の♂の発見は，これら3属の蝶の進化に，かれらの化学的コミュニケーションとともに，新しい解決の光明を投げかけるものと期待される．この珍しい昆虫を求めて，ソロモン群島を訪れることができる鱗翅目研究者がもしおられたら，ぜひ著者まで連絡いただきたい．この蝶のパズルを解くのに必要な，失われた情報を集めるための，最上の方法について話しあえれば幸いである．(文責 編集部)

(Received 5 January 1990)